AMPHISAMYTHA GALAPAGENSIS, A NEW SPECIES OF AMPHARETID POLYCHAETE FROM THE VICINITY OF ABYSSAL HYDROTHERMAL VENTS IN THE GALAPAGOS RIFT, AND THE ROLE OF THIS SPECIES IN RIFT ECOSYSTEMS[1]

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Abstract.—*Amphisamytha galapagensis,* a new polychaete species of the family Ampharetidae, is described from hydrothermal vents of the Galapagos Rift. The placement of *A. galapagensis* in the genus *Amphisamytha* and its relationship with the other two species in the genus are discussed. The developmental biology and ecology of *A. galapagensis* in hydrothermal vent ecosystems are described.

Recently, I examined a collection of ampharetid polychaetes collected by the DSRV/*Alvin* from the Galapagos Rift, situated about 330 km northeast of the Galapagos Islands, and 640 km west of Ecuador. The Rift is part of the world-wide mid-oceanic ridge system where, in certain locales, warm water issues from hydrothermal vents. Crane and Ballard (1980) give a physical description of the Galapagos hydrothermal fields. Such areas often support dense communities of benthic animals, dominated by large vesicomyid bivalve molluscs or by mussels. Other organisms associated with vents include long, tube dwelling, vestimentiferan worms, brachyuran and galatheid crabs, dense aggregations of serpulid polychaetes, eel-like fish, and many other less abundant forms (Galapagos Biology Expedition Participants 1979; RISE Project Group 1980). Free-living chemoautotrophic bacteria, which use energy derived from oxidation of hydrogen sulfide to convert carbon dioxide to organic carbon, most likely serve as the food base for such communities. Bacteria living in trophosomal tissue of the vestimentiferan tube worm, *Riftia pachyptila* Jones, most likely provide nutrients to their host by means of a similar chemoautotrophic process (Cavanaugh *et al.* 1981; Felbeck 1981; Felbeck *et al.* 1981; Jones 1981; Southward *et al.* 1981).

The ampharetid *Amphisamytha galapagensis,* described here for the first time, is a detritivore. The external anatomy, larval development, and the role of this species in hydrothermal vent ecosystems are discussed.

Materials and Methods

Specimens were collected by the submersible DSRV/*Alvin* as follows: 1. Specimens, vacuumed from masses of mussel shells and the bases of vestimentiferan tubes with a "slurp gun," were preserved, and later examined at the surface; 2. Mussel clumps were removed from the bottom with a clam rake and placed in
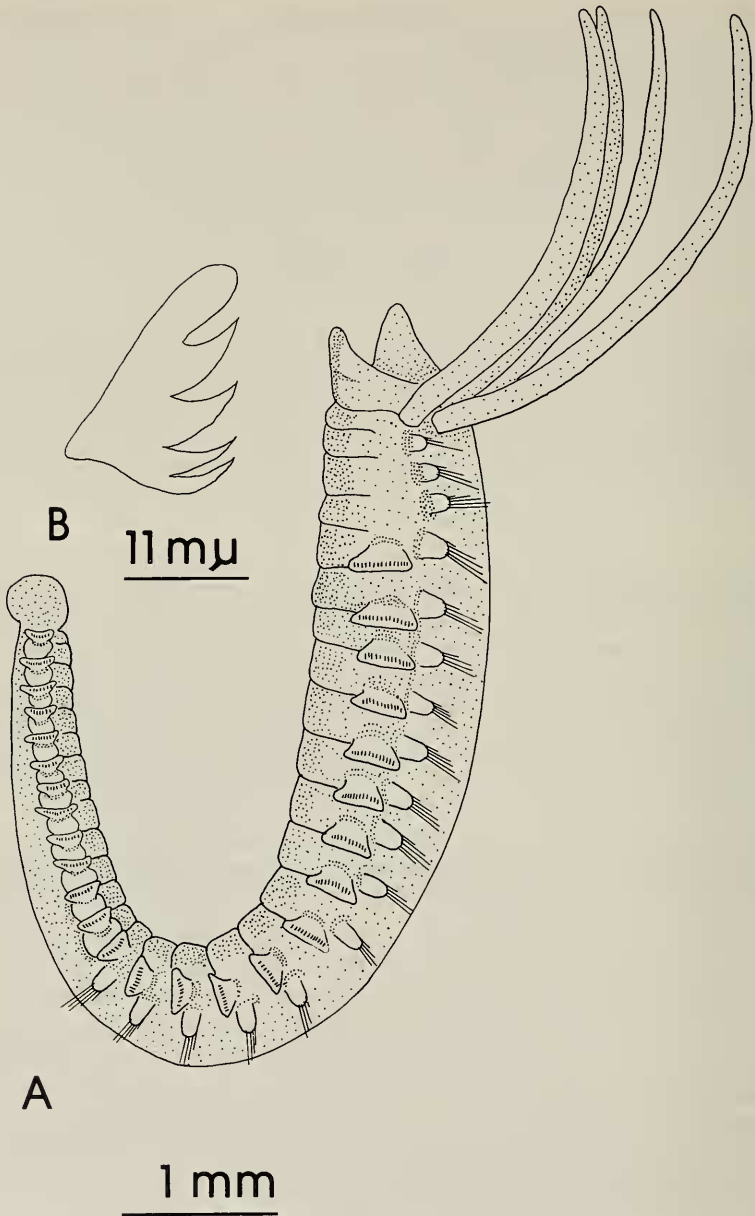

Fig. 1. *Amphisamytha galapagensis*: A, Lateral view of entire worm. Setae start on segment 4. In younger specimens setae may be found on segment 3; B, Mid-thoracic uncinus, lateral view.

an insulated bucket attached to *Alvin*'s basket; at the surface, mussels were rinsed over sieves with mesh openings of 0.297 and 0.88 mm; water left in the insulated bucket was filtered through the same sieves; animals retained on the sieves were preserved and examined at a later time; 3. Vestimentiferan tubes and galatheid crabs were treated in the same manner as mussel clumps.
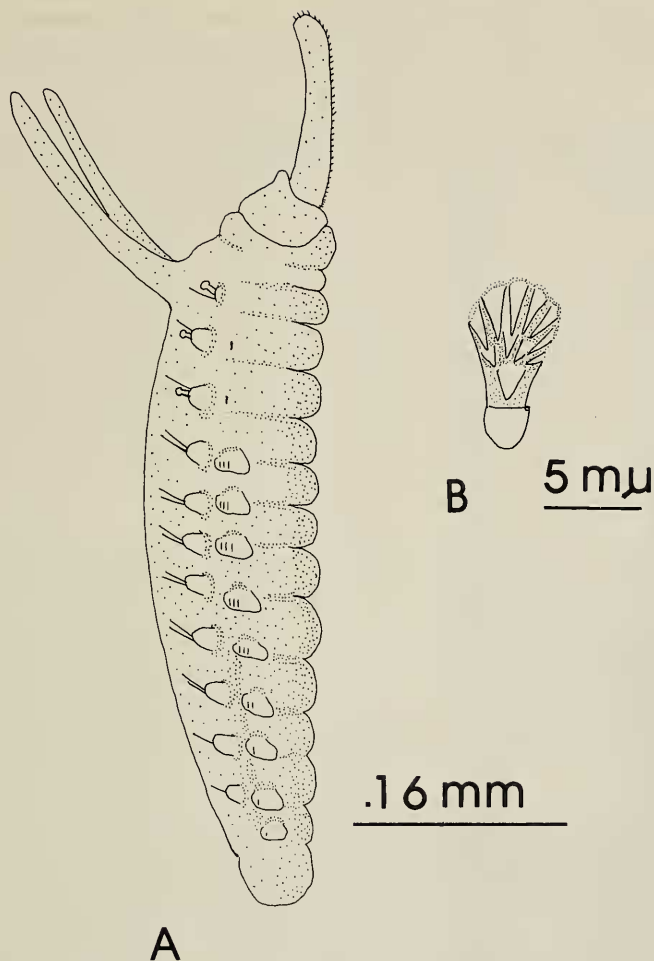
Fig. 2. *Amphisamytha galapagensis*: A, 11-setiger larva, lateral view; B, Larval uncinus, frontal view.

The mechanical devices used to collect vent organisms are described by Galapagos Biology Expedition Participants (1979).

Systematics

Ampharetid polychaetes, for the most part, are wide anteriorly and taper gradually towards the posterior end (Fig. 1A). The prostomium is trilobed. Segments 1 and 2, which lie immediately behind the prostomium, are fused in most species and, ventrally, form the lower lip. Segment 3 is either achaetous or bears two lateral bundles of setae (paleae or winged capillary). Malmgren (1865–1866) and Fauvel (1927) recognized two segments in front of the paleal, making it the third; while Nilsson (1912), Hessle (1917), and Uschakov (1957) recognized one bi-annular segment, making the paleal segment the second. The former numbering system is used here.

Table 1.—Location, number of juveniles and adults, and source of *Amphisamytha galapagensis* examined in this study.

Alvin dive and vent area	Date	Number of specimens[1]		Maximum depth (m)	Source
		A	J		
878: Search for Clambake	11/19/79	0	1	2725	With galatheid crab
879: Mussel Bed	1/20/79	1	2	2495	Mussel washings
880: Mussel Bed	1/21/79	7	18	2493	Mussel washings
883: Garden of Eden	1/25/79	0	6	2493	Slurp gun in mussel area
884a: Garden of Eden	1/25/79	0	11	2482	Clam bucket mussel washings
884b: Garden of Eden	1/25/79	12	3	2482	Rubble residue from mussel area
887: Mussel Bed	2/12/79	3	21	2488	Mussel Bed
888a: Mussel Bed	2/13/79	6	51	2483	Galatheid washings
888b: Mussel Bed	2/13/79	3	7	2483	Galatheid washings
890: Rose Garden	2/15/79	0	9	2447	In jar with two galatheid crabs
891: Garden of Eden	2/16/79	23	24	2488	Rock scrapings
892: Rose Garden	2/17/79	2	9	2454	Residue from cooler
894a: Rose Garden	2/19/79	0	36	2457	—
894b: Rose Garden	2/19/79	1	8	2457	From amphipod trap?
896-22: Rose Garden	2/21/79	26	72	2460	Instant ocean washings
N983: Rose Garden	11/30/79	1	1	2457	Vestimentifera tube washings
N98335: Rose Garden	11/30/79	0	1	2457	Vestimentifera tube washings
N98336: Rose Garden	11/30/79	0	11	2457	Vestimentifera tube washings
N983112: Rose Garden	11/30/79	14	75	2457	Vestimentifera tube washings
N9846: Rose Garden	12/ 1/79	0	4	2451	Vestimentifera tube washings
N9846c: Rose Garden	12/ 1/79	3	6	2451	Vestimentifera tube washings
N9847: Rose Garden	12/ 1/79	0	2	2451	Vestimentifera tube washings
N989: Mussel Bed	12/ 6/79	3	8	2482	Bottle rack washings
N99011: Rose Garden	12/ 7/79	0	1	2451	Vestimentifera tube washings
N99013: Rose Garden	12/ 7/79	1	0	2451	Vestimentifera tube washings
N99014: Rose Garden	12/ 7/79	0	2	2451	Vestimentifera tube washings
N99019: Rose Garden	12/ 7/79	1	1	2451	Vestimentifera tube washings
N99040: Rose Garden	12/ 7/79	0	1	2451	Vestimentifera tube washings
N99041: Rose Garden	12/ 7/79	16	11	2451	Vestimentifera tube washings
N9931: Garden of Eden	12/10/79	7	6	2518	Vestimentifera tube washings
N9932: Garden of Eden	12/10/79	2	0	2518	Vestimentifera tube washings
N9934: Garden of Eden	12/10/79	5	0	2518	Vestimentifera tube washings

Search for Clambake 00°47.92′N, 86°13.5′W
Mussel Bed 00°47.89′N, 86°09.21′W
Garden of Eden 00°47.69′N, 86°07.74′W
Rose Garden 00°48.25′N, 86°13.48′W

[1] A = adult, J = juvenile.

Amphisamytha galapagensis, new species
Figs. 1A, B, 2A, B

Material examined.—See Table 1. Holotype, USNM 81288; 13 Paratypes, USNM 81289.

Description.—Holotype, gravid female, 9.6 mm long, 1.2 mm wide, with 30 setigerous segments. Other specimens up to 10.2 mm long and 1.5 mm wide with 32 setigerous segments. Sexually mature worms as small as 3.6 mm in length. Worms longer than this considered adults. About 300 elliptical eggs, 40–150 μm at their widest point, in body cavity of one 9-mm-long female; 60 eggs at maximum

Table 2.—Number of smooth winged capillary setae per notopodium on "setigerous" segments of the 11- to 18-setiger stages of *Amphisamytha galapagensis*.

Segment	Setiger	Setiger stage						
		11a	11b	14	18a	18b	18c	18d
3	1	3	2	3	2	1	1	0
4	2	3	3	3	3	4	2	5
5	3	3	4	3	4	5	4	6
6	4	3	5	3	5	5	5	6
7	5	3	4	4	4	5	4	6
8	6	3	3	5	6	5	5	6
9	7	3	3	3	6	4	5	6
10	8	3	3	3	3	4	5	7
11	9	3	2	2	4	4	4	7
12	10	2	2	2	5	4	5	7
13	11	1	1	2	4	4	4	7
14	12			1	4	4	4	7
15	13			1	4	3	4	6
16	14			1	4	3	4	7
17	15				4	2	3	7
18	16				2	2	3	7
19	17				2	2	3	6
20	18				2	2	2	5

11a = 0.5 × 0.14 mm 18b = 1.5 × 0.35 mm
11b = 0.7 × 0.18 mm 18c = 1.75 × 0.4 mm
14 = 0.8 × 0.18 mm 18d = 8.0 × 1.2 mm
18a = 1.05 × 0.25 mm

diameter. Color of adult in alcohol white to pale orange. Prostomium indistinctly trilobed, lacking glandular ridges. About 25 smooth, ventrally grooved oral tentacles. Segments 1 and 2 fused, with ventral part forming lower lip. Segment 3 lacking paleae. Minute notopodial lobes with 2–3 short winged capillary setae on segment 3 in juveniles and smaller adults. Each seta approximately 0.25 mm long, 5 μm wide basally, and 6 μm wide across the blade. Four pairs of smooth branchiae about ⅓ of body length, individually inserted, across dorsal surface of segments 3–5. Origin of branchial pairs described in larval development section. Wide gap between branchial groups. Notopodial lobes bearing 6–10 smooth winged capillary setae from segment 4 to end of thorax. Each seta about 0.75 mm long, 10 μm wide basally and 13 μm wide across blade. Notopodia of segments 4 and 5 raised dorsally; notopodia of segment 4 smaller than others. 17 thoracic setigerous segments. Neuropodial lobes (uncinigerous pinnules) each with single row of toothed uncini from segment 7 to end of abdomen. 14 uncinigerous thoracic and 12–15 uncinigerous abdominal segments. Thoracic and abdominal uncini in single transverse rows with, respectively, about 20 and 15 per row in larger specimens. Thoracic and abdominal uncini with 4 teeth in single row above rounded basal prow (Fig. 1B). Larval uncini may be found in juveniles and young adults (Fig. 2B). No notopodial, neuropodial, or anal cirri. Notopodia absent from abdominal segments. Thickened glandular pads above uncinigerous pinnules on most abdominal segments. Pygidium bilobed.

Remarks.—The genus *Amphisamytha* was created by Hessle (1917) to include ampharetids with four pairs of smooth branchiae, no setae on segment 3, no

glandular ridges on the prostomium, 14 thoracic uncinigerous segments and no-topodia on abdominal segments.

Day (1964) considered *Amphisamytha* Hessle (1917) and *Hypaniola* Annekova (1928) to be synonyms of *Lysippides* Hessle (1917). He expanded this genus to include those with or without setae on segment 3. Admittedly the three genera are closely allied; however, the complete lack of setae on segment 3 in larger specimens, I feel, justifies the separation of *Amphisamytha* from these closely related genera.

Amphisamytha galapagensis is distinguished from the other two members of the genus, *A. bioculata* (Moore) and *A. japonica* (Hessle), by the complete lack of anal cirri and by the possession of thick glandular pads above uncinigerous pinnules in most abdominal segments.

Etymology.—Specific name refers to geographic area where specimens were collected.

Feeding

Amphisamytha galapagensis lives in mucus-lined tubes covered by detritus and small chips of volcanic glass, which resemble tubes of the brackish water ampharetids *Hypania invalida* (Grube) and *Hypaniola kowalewskii* (Grimm) (Manoleli 1977). The tubes are attached to solid surfaces such as lava or clam shells.

The morphology of the feeding apparatus of *A. galapagensis* is remarkably similar to that described for the majority of ampharetid species. This suggests a similarity in feeding behavior. Below is a description of feeding behavior, from the sources noted, for *Asabellides oculata* (Webster) and *Hobsonia* (*Amphicteis*) *floridus* (Hartman) (Fauchald and Jumars 1979; personal observations); *Hypania invalida* (Grube) (Manoleli 1975); and *Melinna palmata* (Grube) (Dragoli 1961). In general ampharetids feed by extending tentacles from the tube and over the sediment surface. Mucus, secreted in the ventral part of each tentacle, traps detritus which is carried by ciliary action along the ventral tentacular groove to the mouth. Manoleli (1975) noted that the tentacles are suddenly extended to about three-fourths of the body length from the tube onto the sediment surface; then, laden with detritus, they are gradually retracted towards the mouth, some-times independently of one another. Similar feeding behavior was noted by the author for *A. oculata* (Webster) and by Dragoli (1961) for *M. palmata* (Grube). Although most ampharetids are considered to be detritus feeders, Manoleli (1975) suggested that *H. invalida* (Grube) and *H. kowalewskii* (Grimm) are suspension feeders since phytoplankton is common in gut cavities.

The presence of detritus and bacteria in digestive tracts of juvenile and adult *A. galapagensis* lends support to the idea that mainly they consume particulate matter that settles on solid surfaces; however, suspension feeding cannot be ruled out. The bulk of their food most likely consists of chemoautotrophic bacteria and fecal pellets from other organisms.

Reproduction and Larval Development

Sexually mature worms range from 3.6 to 10.2 mm long and from 0.75 to 1.5 mm wide. Based on observations on other ampharetid species, eggs probably
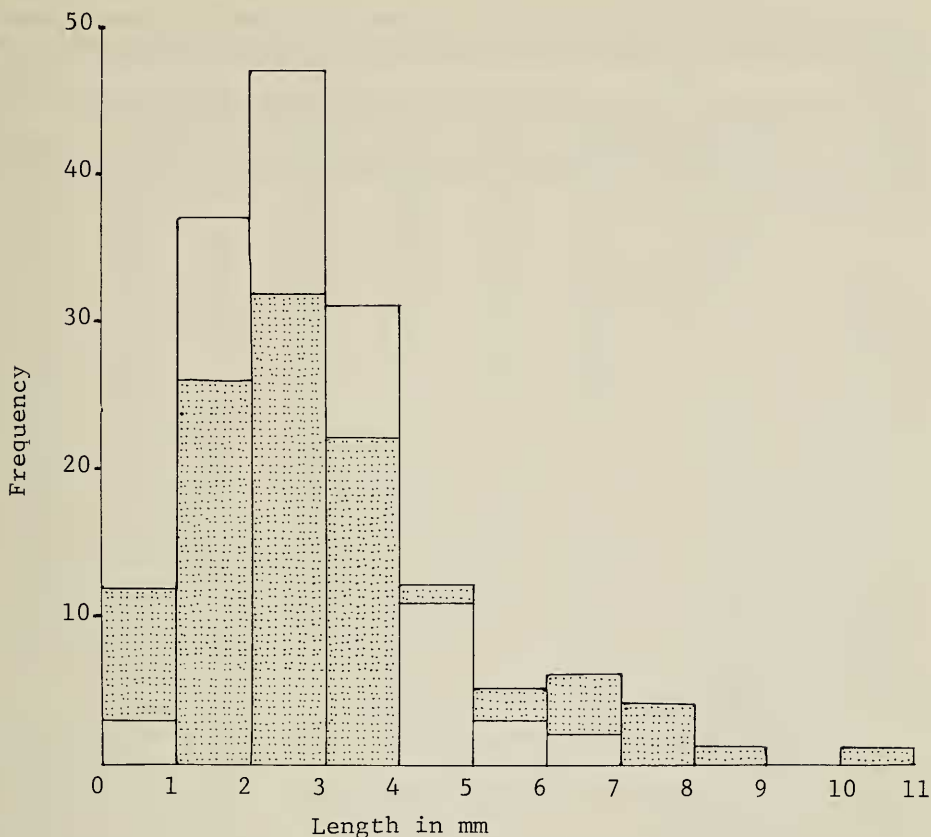
Fig. 3. Frequency histogram for length of a collection of *Amphisamytha galapagensis* from the Rose Garden on *Alvin* dives 890, 892, 894, 896 (clear portion); 983, 894 and 990 (shaded portion). Refer to systematics section for dive locations.

pass singly through nephridia and nephridiopores into the anterior part of the tube where they are fertilized by sperm released by males in the same fashion. Gametes of the ampharetid *Melinna cristata* (Sars) are ejected in two streams from the anterior end of the tube (Nyholm 1950) while Fauvel (1897) indicated that *Ampharete grubei* (Malmgren) and *Amphicteis gunneri* (Sars) shed eggs singly into the water column through two nephridia on the fourth setigerous segment.

Unfertilized eggs, between 40–150 μm maximum width, are irregularly elliptical with a large germinal vesicle. Developing larvae beyond the fertilized egg and prior to the 10-setiger stage were not found. Larval stages in this paper are named on the basis of the number of segments (setigers) bearing capillary setae. In an adult, however, setiger refers to any segment bearing setae of the capillary or uncinate type.

The 11-setiger stage, illustrated in Fig. 2A, is described below. Larval ciliary bands (prototroch, metatrochs or telotroch) were not evident. They disappear at about the 6-setiger stage in *H. floridus* (Hartman), which has similar larval development (Zottoli 1974). There is a single, median, ventrally grooved and ciliated tentacle protruding from the mouth. In the 8-setiger stage of *H. floridus* (Hartman)

Table 3.—Number of larval uncini per uncinigerous pinnule on "setigerous" and "post-setigerous" segments of the 11- to 18-setiger stages of *Amphisamytha galapagensis*. Larval sizes are listed in Table 2.

Segment	Setiger	Setiger stage						
		11a	11b	14	18a	18b	18c	18d
3	1	0	0	0	0	0	0	0
4	2	1	0	0	0	0	0	0
5	3	1	1	0	0	0	0	0
6	4	3	1	1	0	0	0	0
7	5	3	1	1	5	2	7	0
8	6	3	2	4	5	3	7	0
9	7	3	2	4	4	3	6	0
10	8	2	2	3	4	3	4	0
11	9	2	2	3	4	2	3	0
12	10	1	1	2	4	2	3	0
13	11	1	1	2	3	3	3	0
14	12	1	1	2	3	3	3	0
15	13	1	1	1	3	3	3	0
16	14			1	3	3	3	0
17	15			1	3	2	3	0
18	16			1	3	2	3	0
19	17				2	3	3	0
20	18				2	3	3	0
	"Post-setiger" (abdomen)							
21	1				2	6	5	0
22	2				2	5	5	0
23	3					5	4	0
24	4					4	4	0
25	5					3	2	0
26	6					2	1	0
27	7					1	1	0
28	8							0
29	9							0
30	10							14
31	11							10
32	12							6
33	13							6

this tentacle is used in feeding, and detrital particles, bound in mucus secreted at the tentacle tip, are transported by ciliary action along the ventral groove to the mouth. Prostomial eyespots are lacking and fused segments 1 and 2 lie immediately behind prostomium. Segments 3–5 bear small notopodia, each with one spatulate and one smooth winged capillary seta. Spatulate setae are larval structures formed only in notopodia of the first three setigers. They disappear in later stages. Similar setae were described by Wilson (1928) on the first 11 setigers of the terebellid polychaete *Loimia medusa* (Savigny). One uncinus is embedded in the epidermis on each side of segments 4 and 5 below the notopodia. Each uncinus bears about 6–10 teeth above a single tooth and rounded basal part (Fig. 2B). Segments 6–13 each bear a pair of notopodia bearing smooth, winged capillary setae (Table 2). Uncinigerous pinnules, each have larval uncini on segments 7–

Table 4.—Number of adult uncini per uncinigerous pinnule on "setigerous" and "post-setigerous" segments of the 11- to 18-setiger stages of *Amphisamytha galapagensis*. Larval sizes are listed in Table 2.

Segment	Setiger	Setiger stage						
		11a	11b	14	18a	18b	18c	18d
3	1	0	0	0	0	0	0	0
4	2	0	0	0	0	0	0	0
5	3	0	0	0	0	0	0	0
6	4	0	0	0	0	0	0	0
7	5	0	0	0	0	5	1	18
8	6	0	0	0	0	6	1	18
9	7	0	0	0	0	4	2	22
10	8	0	0	0	0	4	3	25
11	9	0	0	0	0	3 .	2	23
12	10	0	0	0	0	3	3	20
13	11	0	0	0	0	3	3	17
14	12			0	0	2	3	20
15	13			0	0	2	2	19
16	14			0	0	2	2	19
17	15				0	2	2	18
18	16				0	3	2	17
19	17				0	1	2	15
20	18				0	1	1	14
	"Post-setiger" (abdomen)							
21	1					0	0	15
22	2					0	0	14
23	3					0	0	15
24	4					0	0	15
25	5					0	0	13
26	6					0	0	14
27	7					0	0	14
28	8							14
29	9							15
30	10							2
31	11							0
32	12							0
33	13							0

13 (Fig. 2A, Table 3). First and only pair of branchiae originate from dorsal surface of segment 3. As growth continues the uncini disappear from segments 4 and 5.

In the 14-setiger stage, the second pair of branchiae arise behind the first on dorsal surface of segment 4; larval uncini disappear from segment 6.

The following changes take place between the stages above and adult worms: 1) Smooth winged capillary setae on segment 3 are lost. This suggests that possession of setae on segment 3 is a primitive character in the family Ampharetidae. 2) Abdominal segments increase in number to 12–15. 3) Larval spatulate setae are lost. 4) Uncini change in number and structure: a) There is an increase in number of adult uncini per uncinigerous pinnule (Fig. 1B, Table 4) coinciding

with a decrease in number of larval uncini (Fig. 2B, Table 4). Uncini are first formed in the dorsal part of each pinnule. b) As new uncini are formed, older ones are pushed ventrally. Usually, one developing uncinus is visible in each abdominal uncinigerous pinnule of young worms. Uncini of the maldanid poly-chaetes *Clymenella torquata* (Leidy) and *Euclymene oerstedi* (Claparede) are formed ventrally rather than dorsally as above (Pilgrim 1977). This character may aid in determining general evolutionary relationships between polychaete fami-lies. Length of individual *A. galapagensis* uncini in each row increases slightly from ventral to dorsal supporting the idea that uncini move along the row. Pilgrim (1977:294) made the point that in maldanids, "the difference in length between ventral and dorsal chaetae *in older worms* becomes an indicator of their rate of progress along the row, and presumably of the growth rate of the whole body, the greater difference in length, the lower the growth rate." As uncini of *A. galapagensis* differ slightly in length along each row, a rapid growth rate is sug-gested. Larval uncini are still present in the ventral part of adult posterior ab-dominal uncinigerous pinnules. Since newly formed uncini are of the adult type, the presence of larval uncini suggests that once a particular size is reached, growth slows. This would allow food reserves to be used for gamete production and development, rather than growth, thus enhancing the reproductive potential of the population. 5) A fourth pair of branchiae appears on dorsal surface of segment 5. 6) Up to 25 smooth, ventrally grooved and ciliated, oral tentacles are developed.

Development of this species is similar to that of the ampharetids *A. grubei* Malmgren (Thorson 1946), *H. floridus* (Hartman) (Zottoli 1974), *M. cristata* (Sars) (Nyholm 1950), and *Schistocomus sovjeticus* Annekova (Okuda 1947).

Environmentally predictable deep-sea communities are inhabited for the most part by k-selected species, characterized by low reproductive potentials, long life spans, and long maturation periods (Sanders and Hessler 1969; Sanders 1979). One might predict, therefore, that numbers and biomass of juveniles in the deep-sea would tend to be lower than those of adults over a given time span. This hypothesis is supported by data on deep-sea bivalves (Grassle and Sanders 1973), two isopod species (Hessler 1970), one species of tanaid (Gardiner 1975), and certain large bathypelagic euphausiids (Mauchline 1972). The deep-sea brittle-star *Ophiura ljungmani* (Lyman), however, is an exception to this rule (Tyler and Gage 1980).

Lonsdale (1977) observed large numbers of dead mussels in certain vent areas suggesting that this unique environment is unstable. Instability tends to favor opportunistic or r-selected species (Grassle and Grassle 1974) that are character-ized by high reproductive rate, short maturation time, short life span, large pop-ulation size, high mortality rate, wide physiological tolerances and broad cos-mopolitan distributions (Sanders 1979). High reproductive rates allow opportunists to increase numbers under favorable conditions, thus enhancing their ability to colonize new areas, and ensure survival of the species. The deep-sea wood boring bivalve *Xylophaga* (Turner 1973), the ampharetid polychaete *Decemunciger,* as-sociated with *Xylophaga* (Zottoli 1982), possibly the Galapagos Rift vesicomyid clams (Turekian and Cochran 1981) and undescribed mussels (Rhoads *et al.* 1981) have these characters more than many other deep-sea organisms.

The presence of numerous (300) small eggs (150 μm maximum diameter) in the

body cavity of some female worms and the presence of numerous juveniles in most samples (Fig. 3) imply a high reproductive rate and suggest that *A. galapagensis* is relatively opportunistic. Long planktonic development associated with opportunism would improve the chances of worms reaching and colonizing new vent areas. Egg size is often suggestive of whether or not a species has planktonic development. Thorson (1951) suggested that polychaete species with egg diameters less than 150 μm generally have long pelagic planktotrophic development. This generalization does not apply to most ampharetids investigated to date. *H. floridus* (Hartman) (Zottoli 1974), *H. kowalewskii* (Grimm) (Marinescu 1964) and *Melinnexis arctica* Annekova (Annekova 1931), which have eggs roughly the same width as *A. galapagensis,* retain developing larvae in the maternal tube until they are able to crawl on the bottom. Eggs of *Alkamaria romijni* Horst, a protandric hermaphrodite, either develop in the body cavity or in the maternal tube (Wesenberg-Lund 1934). On the basis of its similarity to the above mentioned ampharetids, it is here hypothesized that *A. galapagensis* produces larvae that swim or crawl along the bottom in the area where they were released. This would allow continuous repopulation without relying on larvae from geographically separated areas. As regards emigration to new sites, larvae would probably be swept by bottom currents to new vent areas. Lonsdale (1977) recorded a current speed of 18 cm/sec along the bottom in a vent area on the East Pacific Rise. Cold water would reduce the metabolic rate as larvae are swept away from warm vent areas, thereby prolonging survival time and enhancing the chances of reaching a new vent site.

Acknowledgments

Literature Cited

Annekova, N. 1928. Über die pontokaspischen Polychaeten. 2. Die Gattungen *Hypaniola, Parhypania, Fabricia* und *Manajunkia*.—Annuaire du Musée Zoologique de l'Academie des Sciences de l'URRS 30:13–20.

———. 1931. Zur Polychaetenfauna von Franz-Joseph-Land (*Melinnexis* gen. nov. *arctica* sp.n.).—Zoologischer Anzeiger, Leipzig 95:269–272.

Cavanaugh, C. M., S. L. Gardiner, M. L. Jones, H. W. Jannasch, and J. B. Waterbury. 1981. Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: Possible chemoautotrophic symbionts.—Science 213:340–342.

Crane, K., and R. D. Ballard. 1980. The Galapagos Rift at 86°W: 4. Structure and morphology of hydrothermal fields and their relationship to the volcanic and tectonic processes of the Rift Valley.—Journal of Geophysical Research 85(B3):1443–1445.

Day, J. H. 1964. A review of the family Ampharetidae (Polychaeta).—Annals of the South African Museum 48(4):97–120.

Dragoli, A. L. 1961. Peculiar feeding habits in the Black Sea polychaete *Melinna palmata* Grube.—Doklady Akademii Nauk SSR 138(4):970–973. [In Russian.]

Fauchald, K., and P. A. Jumars. 1979. The diet of worms: A study of polychaete feeding guilds.—Oceanography Marine Biology Annual Review 17:193–284.

Fauvel, P. 1897. Recherches sur les Ampharétiens, Annélides polychètes sédentaires. Morphologie,

Anatomie, Histologie, Physiologie.—Bulletin Scientifique de la France et de la Belgique 30: 277–488.

———. 1927. Polychètes Sédentaires.—Faune de France 16:1–494.

Felbeck, H. 1981. Chemautotrophic potential of the hydrothermal vent tube worm *Riftia pachyptila* Jones (Vestimentifera).—Science 213:336–338.

———, J. J. Childress, and G. N. Somero. 1981. Calvin-Benson cycle and sulphide oxidation enzymes in animals from sulphide-rich habitats.—Nature 293:291–293.

Galapagos Biology Expedition Participants. 1979. Galapagos '79: Initial findings of a deep-sea biological quest.—Oceanus 22(2):2–10.

Gardiner, L. F. 1975. The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea).—Smithsonian Contributions to Zoology 170:1–265.

Grassle, J. F., and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes.—Journal of Marine Research 32:253–284.

———, and H. L. Sanders. 1973. Life histories and the role of disturbance.—Deep-Sea Research 20:642–659.

Hessle, C. 1917. Zur kenntnis der terbellomorphen Polychaeten.—Zoologische Bidrag från Uppsala 5:39–258.

Hessler, R. R. 1970. The Desmosomatidae (Isopoda, Asellota) of the Gay Head-Bermuda transect.—Bulletin of the Scripps Institution of Oceanography 15:1–185.

Jones, M. 1981. *Riftia pachyptila* Jones: Observations of the vestimentiferan worm from the Galápagos Rift.—Science 213:333–336.

Lonsdale, P. 1977. Clustering of suspension feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers.—Deep-Sea Research 24:857–863.

Malmgren, A. J. 1865–1866. Nordiska Hafs-Annulater.—Öfversigt Svenska Vetenskaps Akademiens Förhandlingar 22:181–192, 355–410.

Manoleli, D. 1975. On the distribution, biology and origin of polychaeta from the Danube and Danube delta.—Travaux du Muséum d'Histoire Naturelle "Grigore Antipa" 16:25–34.

———. 1977. La structure, la texture et la composition minéralogique des tubes de *Hypania invalida* et *Hypaniola kowalewskii* (Polychaeta, Ampharetidae) du Danube. Travaux du Muséum d'Histoire Naturelle "Grigore Antipa" 28:9–15.

Marinescu, V. P. 1964. La reproduction et le développement des polychètes reliques Ponto-Caspiens du Danube: *Hypaniola kowalewskii* (Grimm) et *Manayunkia caspica*.—Revue Roumaine de Biologie, Série de Zoologie 9:87–100.

Mauchline, J. 1972. The biology of bathypelagic organisms, especially Crustacea.—Deep-Sea Research 19:753–780.

Nilsson, D. 1912. Beiträge zur kenntnis des nervensystems der polychaeten.—Zoologiska Bidrag från Uppsala 1:85–161.

Nyholm, K. 1950. Contributions to the life-history of the ampharetid, *Melinna cristata*.—Zoologiska Bidrag från Uppsala 29:79–91.

Okuda, S. 1947. On an ampharetid worm, *Schistocomus sovjeticus* Annekova, with some notes on its larval development.—Journal Faculty Science Hokkaido Imperial University (ser. 6) 9:321–329.

Pilgrim, M. 1977. The functional morphology and possible taxonomic significance of the parapodia of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi*.—Journal of Morphology 152:281–302.

Rhoads, D. C., R. A. Lutz, E. C. Revelas, and R. M. Cerrato. 1981. Growth of bivalves at deep-sea hydrothermal vents along the Galápagos Rift.—Science 214:911–913.

RISE Project Group. 1980. East Pacific Rise: Hot springs and geophysical experiments.—Science 207:1421–1444.

Sanders, H. L. 1979. Evolutionary ecology and life-history patterns in the deep-sea.—Sarsia 64:1–7.

———, and R. R. Hessler. 1969. Ecology of the deep-sea benthos.—Science 163:1419–1424.

Southward, A. J., E. C. Southward, P. R. Dando, G. H. Rau, H. Felbeck, and H. Flügel. 1981. Bacterial symbionts and low $^{13}C/^{12}C$ ratios in tissues of Pogonophora indicate unusual nutrition and metabolism.—Nature 293:616–620.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates,

with special reference to the planktonic larvae in the Sound (Øresund).—Meddeleser Fra Kommissionen for Danmarks Fiskeri-og Havundersogelser, serie: Plankton 4(1):1–523.

———. 1951. Zur jetzigen lage der marinen bodentierökologie.—Verhandlungen der Deutschen Zoologischen Gesellshaft 12(17):276–326.

Turekian, K. K., and J. K. Cochran. 1981. Growth rate of a vesicomyid clam from the Galápagos spreading center.—Science 214:909–911.

Turner, R. D. 1973. Wood-boring bivalves, opportunistic species in the deep-sea.—Science 180: 1377–1379.

Tyler, P. A., and J. D. Gage. 1980. Reproduction and growth of the deep-sea brittlestar *Ophiura ljungmani* (Lyman).—Oceanolica Acta 3(2):177–185.

Uschakov, P. V. 1957. Bristleworms of the far eastern seas of USSR (Polychaeta). Opredeliteli po faune SSSR (Keys to the fauna of the USSR) 56:1–445. [In Russian.]

Wesenberg-Lund, E. 1934. A viviparous brackish-water ampharetid, *Alkmaria romijni* Horst from Ringkøbing Fjord.—Videnskabelige Meddelelser Naturhistorisk Forening 98:215–222.

Wilson, D. P. 1928. The post-larval development of *Loimia medusa* Sav.—Journal of the Marine Biological Association of the United Kingdom 15(1):129–147.

Zottoli, R. A. 1974. Reproduction and larval development of the ampharetid polychaete *Amphicteis floridus*.—Transactions of the American Microscopical Society 93(1):78–89.

———. 1982. Two new genera of deep-sea worms of the family Ampharetidae and the role of one species in deep-sea ecosystems.—Proceedings of the Biological Society of Washington 95(1): 48–57.

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